

ANATOMY OF THE PALM RHAPIS EXCELSA,
III. JUVENILE PHASE

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IN THE FIRST PAPER of this series (Zimmermann & Tomlinson, 1965) we showed that in the adult aërial stem of *Rhapis excelsa* all vascular bundles maintain their individuality and proceed indefinitely through the stem. At intervals, each vertical bundle becomes a leaf trace, but gives off another vertical bundle prior to its departure into the leaf. The number of vertical bundles given off by a leaf trace can vary from zero to two or more, although it is normally one. This means that the number of bundles throughout the length of the stem does not necessarily have to remain constant. Indeed, such changes have been described by Strasburger (1906); they are, however, not great, the number remaining well within the same order of magnitude. In the seedling the situation is quite different. Before the palm can begin its growth in height it has to establish the stem diameter; and the number of vascular bundles has to increase several orders of magnitude. It is the purpose of this paper to account for the multiplication of vascular bundles in the aërial axis as it enlarges by primary growth, following the establishment of the seedling.

The phase of development which succeeds the establishment of the seedling is developmentally and morphologically quite distinct from the subsequent vegetative and reproductive phases; it has, therefore, been referred to as the "juvenile phase" (Tomlinson, 1964). In most palms morphological features of this phase include juvenile leaves (Tomlinson, 1960), leaves transitional to the adult type of foliage, numerous adventitious roots and, in multiple-stemmed palms, lateral vegetative branches. These are all borne on an obconical axis in which the internodes are usually much congested.

Literature on early stages of growth in palms is extensive, but deals almost exclusively with the germination of the seed, its early development, and with the anatomy and morphology of the seedling (e.g., Von Mohl, 1824; Gatin, 1906, 1912). Anatomical studies have been restricted to the vascular system of cotyledon, first plumular leaves, and the vascular transition between seedling, root, and stem (e.g., Gehrke, 1887; Micheels, 1889; Schlickum, 1896; and more recently Ginieis, 1952). The gross morphology of later stages has been considered by Karsten (1856). Unfortunately, our literature search has revealed no specific information about the seedling of *Rhapis excelsa*.

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The significance of the post-seedling or juvenile phase of growth in the development of palms and other monocotyledons seems to have been little appreciated. An attempted analysis of the vascular system of the seedling of *Trachycarpus* by Suessenguth (1921, p. 50) is incorrect since it is based on theoretical principles which we now know are quite mistaken (Tomlinson & Zimmermann, 1966a). Helm (1937) discusses growth of palm seedlings in terms of the establishment of the primary thickening meristem which maintains the massive primary axis of the palm in the adult stage. The primary thickening meristem is essentially the end result of the juvenile phase of growth. That this phase of growth has been overlooked is indicated by the absence of any English term to describe it. It was not until 1936 that Troll first clearly distinguished the initial axial development of the juvenile phase as "Erstarkungswachstum" ("strengthening growth") from the continuing "Primärdickenwachstum" ("primary thickening growth") which maintains the diameter of the adult palm stem *after* the maximum diameter of the stem has been established in the juvenile phase (see also the discussion in Helm, 1937). Both German terms did exist prior to 1936 but they were used indiscriminately to describe primary thickening growth. Since the literal translation of the German word "Erstarkungswachstum" would be somewhat misleading, we suggest the term *establishment growth* for the type of growth in the juvenile phase which leads to the establishment of the primary thickening meristem. Since this type of growth involves the production of internodes with successively greater diameters, it produces an inverted conical structure.

This type of growth is exhibited by *Rhapis* which is suitably small for microscopic analysis. The only previous illustration of the vascular system in the juvenile axis of a palm is one of the coconut by Von Mohl (1824, *Fig. Q3*) which does not, however, throw light on the problem of vascular bundle multiplication. Our own study of the juvenile phase of *Rhapis* is concerned solely with this problem in structural terms.

MORPHOLOGY OF THE JUVENILE AXIS

Plants of the age investigated are illustrated in FIG. 1A. Earlier stages of seedling development are not shown. At the age illustrated the obconical outline of the axis is obscured by the development of numerous adventitious roots and vegetative branches. The latter arise from buds in the axils of basal leaves and grow out in order of their age (buds and suckers numbered in FIGS. 1B and C, 1 being youngest). Branches grow out as short rhizome segments (FIG. 1C) thereby initiating the sympodial rhizome system described in the second paper of this series (Tomlinson & Zimmermann, 1966b). In the aerial parent axis the transition to the adult vegetative phase is marked by elongation of the most distal internodes, once the maximum diameter has been reached (FIG. 1B). This transition is associated with suppression of axillary buds. No roots are

borne on the distal part of the stem. Buds only recur distally in the reproductive phase as inflorescences which are often aborted.

MATERIALS AND METHODS

Propagation of *Rhapis excelsa* is normally by rhizome offsets because viable seeds are not readily available in South Florida. We are, therefore, indebted to Mr. Mulford B. Foster of Orlando, Florida, who generously supplied several 6-month-old seedlings on which this investigation is based. These were cultivated at the Fairchild Tropical Garden for an additional 6 to 18 months until they were fixed, at the age of 1 to 2 years, for anatomical study.



FIGURE 1. Morphology of juvenile phase in *Rhapis excelsa*. A. General habit of 1-year-old seedling, $\times 1/8$. B. Base of same axis, leaves removed, $\times 2$; early stages in development of axillary suckers. C. Older, more vigorous seedling, $\times 1/4$; rhizomatous development of axillary suckers. In B and C, 1-7 indicate successive axillary suckers which develop in order of their age, 1 youngest, 7 oldest.

For microscopic analysis, continuous serial sections 30 μ thick of two seedling axes were cut on the sliding microtome and stained in safranin and Delafield's haematoxylin, as described previously. A complete series of sections was mounted, not every tenth as in previous studies, because the congested vascular system could only be understood by photographing each section. Each section was mounted on a separate slide, as is now our standard practice, in order that the optical shuttle method of aligning successive sections in the camera frame could be used (Zimmermann & Tomlinson, 1966). Photography of serial microtome sections was again supplemented by direct photography of successive surface cuts of seedlings clamped in the sliding microtome.

GENERAL ANATOMY OF THE JUVENILE AXIS

Over-all increase in diameter of the axis in the juvenile phase of growth of *Rhapis* is illustrated in FIGS. 2-4, representing sections at successively higher levels from one of the microtome series. Increase in certain dimensions in the same series is given in TABLE I.

TABLE I. Increase of Certain Dimensions in the Seedling Axis of *Rhapis excelsa*

Slide number	Level (mm.)	Average cortex diam. (mm.)	Central Cylinder			
			Av. diam. (mm.)	Approx. no. vascular bundles	Av. diam. vascular bundles	
					Periphery μ	Center μ
1 (FIG. 2A)	0	0.8	0.7	8	—	—
50 (FIG. 2B)	1.5	1.2	1.4	38	150	150
101 (FIG. 2C)	3.0	2.0	2.4	82	150	180
200 (FIG. 3)	6.0	1.6	5.5	160	300	240
349 (FIG. 4)	10.5	1.3	8.0	400	450	330

Axis outline irregular owing to distortion imposed by numerous root and branch insertions. Surface layers either resembling those of rhizome, or more usually with irregular divisions, but without a regular phellogen, cells ligno-suberized, abundantly tanniniferous and forming an irregular periderm. Cortex very wide in lowest levels and exceeding central cylinder, but becoming proportionately narrower in higher levels (TABLE I). Cortical ground parenchyma irregular, outer layers compact, small-celled; inner layers less compact, often showing evidence of belated radial enlargement especially in association with branch insertions. Cortical fibrous strands well developed at all except very lowest levels, fibrous strands up to 120 μ wide, largest including narrow central vascular elements. Innermost cortical layers often free of fibrous strands. Central cylinder not delimited by endodermis or other specialized layer but by irregular region of somewhat congested vascular bundles. Central vascular bundles not congested. Vascular bundles irregular in transverse outline, leaf traces recognized by oblique, often more or less horizontal passage from central cylinder through cortex. Diameter of bundles increasing upwards (TABLE I),

largely due to increase in amount of fibrous sheathing tissue, especially in peripheral bundles (cf. FIGS. 2-4). Metaxylem elements narrow, irregular, indistinct from protoxylem at lowest levels. Starch abundant in ground parenchyma except at periphery of cortex. Tannin cells mostly restricted to outer cortex. Stegmata (silica cells) common next to fibers of bundles in both cortex and central cylinder.

COURSE OF VASCULAR BUNDLES

Although complex, the distribution of vascular bundles can be interpreted readily in the light of our analysis of the vascular system in the aërial stem. The close interlinking of trace systems from roots and branches,² indicative of a close developmental relation, does not obscure the vascular system of the axis itself. Vascular systems of central cylinder and cortex remain distinct, although less so than in rhizome and aërial stem.

1. CENTRAL CYLINDER. Cinematographic analysis reveals frequent *leaf traces* passing more or less horizontally into leaves, and readily distinguished from the numerous *vertical bundles* cut more or less transversely in transverse sections. Vertical bundles are transformed into leaf traces by change from a vertical to a horizontal course. The constant relation between leaf traces and continuing vertical bundles which was found in the aërial stem does not exist in the seedling axis. This is discussed later. In addition to this main vascular system there is an interlinking network of usually narrow bundles which correspond to the bridges of the adult stem. They are sufficiently extensive to be referred to as an *anastomosing bridge system*.

Vertical bundles. Traced upwards, the distance of vertical bundles from the periphery of the central cylinder increases so that the bundles come to occupy the uncrowded center of the stem, prior to their conversion into leaf traces. This apparent displacement is largely the result of the widening of the central cylinder in the obconical axis. Vertical bundles may even diverge from the stem center, but at a shallower angle than the limit of the central cylinder. The helical pathway of the central bundles which is characteristic of the aërial stem is established early and again it corresponds in direction (but not in magnitude) to the phyllotactic spiral.

Leaf traces. Vertical bundles become leaf traces by an abrupt change to an approximately horizontal direction. Unlike the bundles of the adult axis, however, there is no fixed relation between leaf traces and continuing vertical bundles. In the lowest internodes where there are few bundles, the vertical part of each bundle is short and all bundles diverge from

² Insertion of root and branch traces will be described in detail in a later paper in this series.

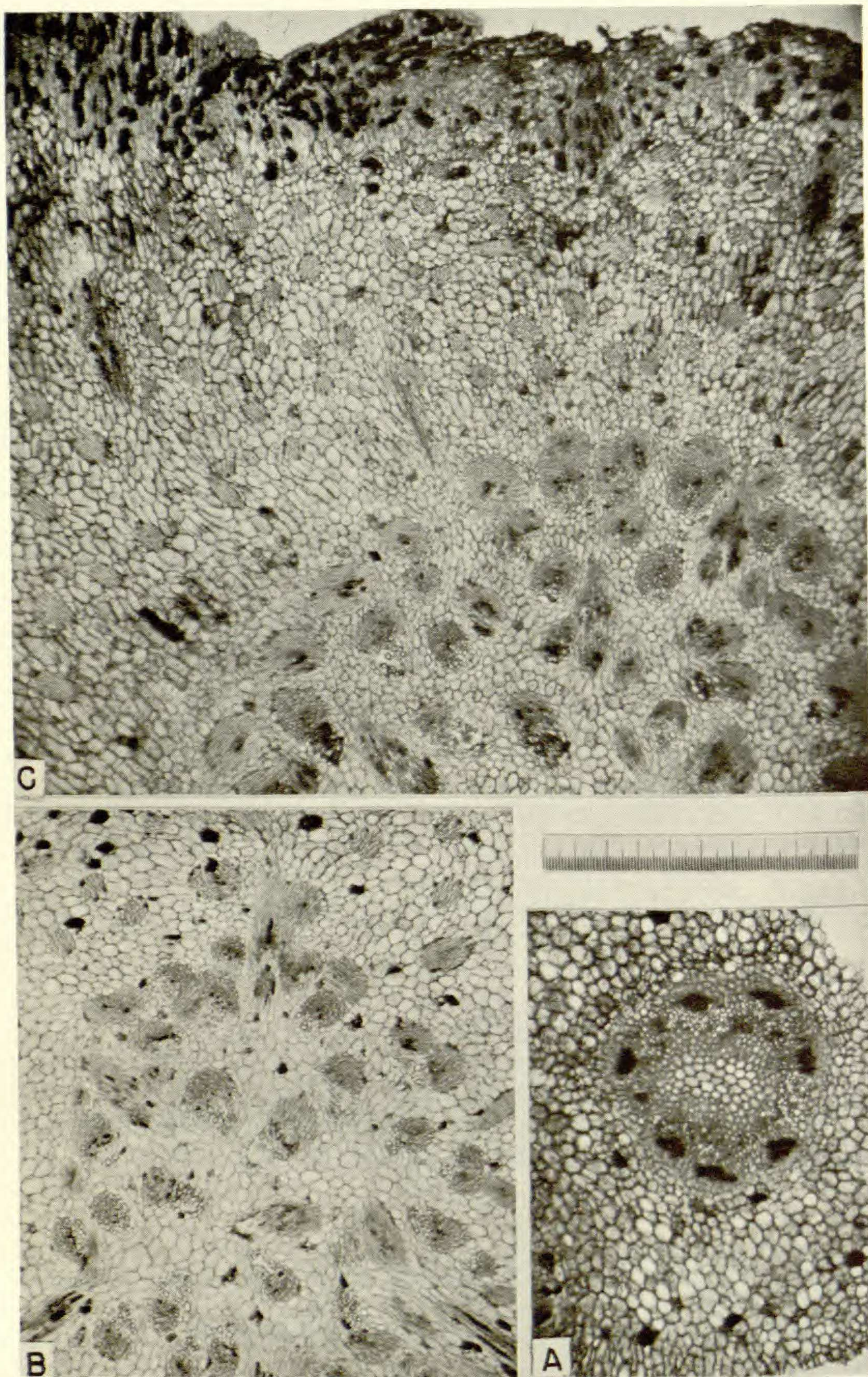


FIGURE 2. Transverse sections of a juvenile axis of *Rhaps excelsa* at successively higher levels. A. At approximate level of cotyledonary node. B. 1.5 mm. above A. C. 3 mm. above A. Scale equals 1 mm.

about the same depth in the stem center. Distally, as the total number of bundles increases, the length of the vertical part of the bundles' course rapidly increases and differences between major, intermediate, and minor leaf traces become evident as the trace complement to each leaf becomes larger.

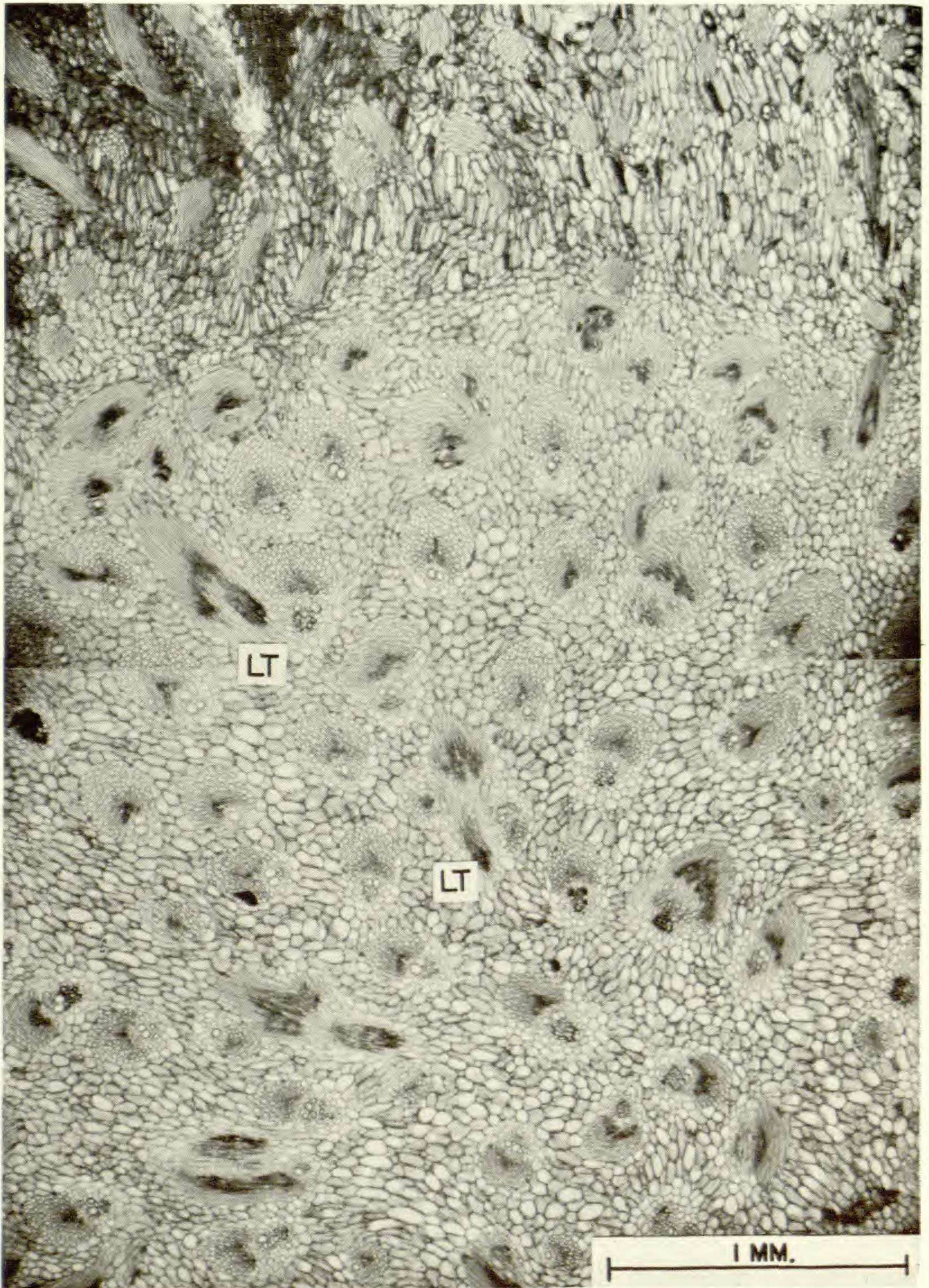


FIGURE 3. *Rhaps excelsa*, same axis as illustrated in FIG. 2, 6 mm. above 2A, same magnification. Two leaf traces (LT) indicated, the one in the center of the figure with two recently derived bridges.

Anastomosing bridge system. As in the adult axis departure of a leaf trace is associated with the development of bridges which are very pronounced in the juvenile phase. The first bridge originates as the vertical bundle turns outward as a recognizable leaf trace in the stem center. Subsequently more (up to 10) originate as the leaf trace passes through the crowded periphery. Bridges may even be given off by the leaf trace as it passes through the cortex, such bridges becoming incorporated into the cortical system. Bridges in the juvenile axis resemble those of the adult stem in diverging upwards from a leaf trace and often linking immediately with a nearby vertical bundle. Otherwise they may differ in three important respects: (a) they are often very long, extending irregularly without interruption through several internodes; (b) they commonly split; (c) they, or their branches, ultimately join vertical bundles or reach the periphery of the central cylinder where they become vertical bundles. Bridge bundles are narrow, with inconspicuous vascular elements although the largest resemble peripheral vertical bundles in the base of the stem. Small bridges may lack vascular tissue and appear as narrow fibrous strands. From the manner in which they diverge, upwards from leaf traces, these bridge bundles seem developmentally homologous with those of the aërial stem but their ramifications and extensive development justify referring to them as an anastomosing system. Root and branch traces connect extensively with these bridges or their branches.

2. CORTEX. The cortical system of fibrous bundles remains largely independent of the central system. Cortical bundles traced downwards from the leaves anastomose freely to form a reticulum but many bundles end blindly below. The reticulum is much distorted around branch and root insertions. Interconnection between vascular systems of cortex and central cylinder is somewhat more pronounced than in the rhizome and aërial stem, either because of direct interchange of vascular bundles between the innermost region of the cortex and the periphery of the central cylinder or because leaf traces, as they pass across the cortex, link with the cortical reticulum via bridges.

MULTIPLICATION OF VASCULAR BUNDLES

We come now to the most interesting anatomical aspect of the juvenile axis, namely the question of how the increase in number of vascular bundles is accomplished during establishment growth. In TABLE I it can be seen that during a height increase of 10.5 mm. the seedling axis had increased from 0.7 to 8 mm. in diameter (central cylinder) and from 8 to 400 vascular bundles. Thorough study of numerous motion picture sequences have revealed the following processes.

Ultimate branches of the anastomosing bridge system reach the periphery of the central cylinder, turn erect there and become vertical bundles. Each leaf trace thus contributes (via the anastomosing system) on the average more than one vertical bundle. In the higher levels of the seed-

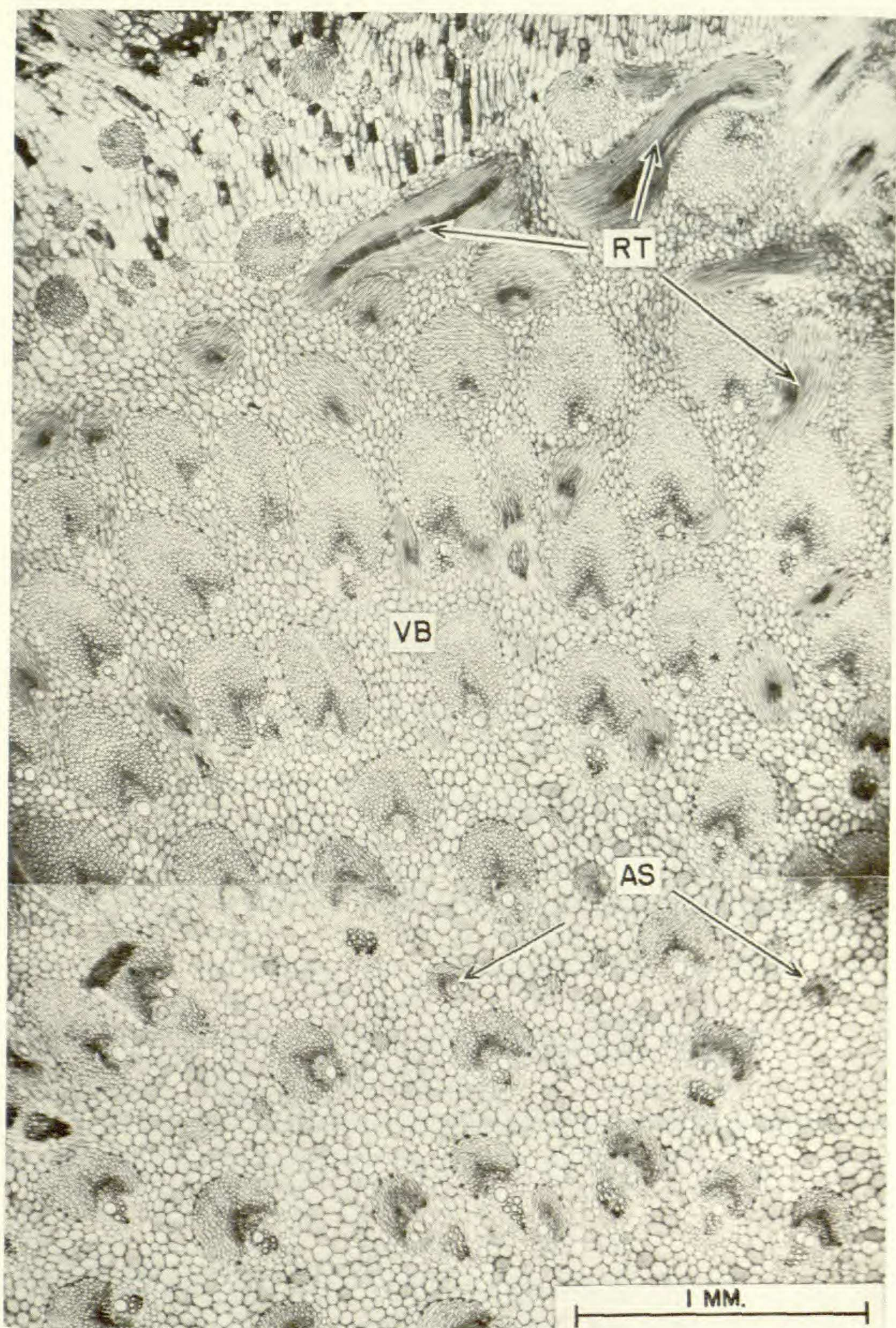


FIGURE 4. *Rhapis excelsa*, same axis as illustrated in FIG. 2, 10.5 mm. above 2A, same magnification. This now closely resembles adult stem, peripheral vertical bundles (VB) with well-developed fibrous sheaths. Bundles of the anastomosing bridge system (AS), root traces (RT).

ling axis the anatomy resembles more and more the mature vegetative stem (FIG. 4), leaf traces giving off several bridges and vertical bundles. In principle then, the increase in number of vascular bundles in the post-seedling stage is accomplished by the same mechanism by which the number of vascular bundles in the mature stem can be varied, i.e., by the variable number of vertical bundles which is given off by each leaf trace.

It must be emphasized that production of additional vertical bundles is a property of the periphery of the central cylinder. No vertical bundles are developed in the stem center. We have also seen occasional vertical bundles split in the peripheral region. It is quite clear that the system of vertical bundles becomes "directed" and "stabilized" in the peripheral region. This must be based upon the way in which the vascular system is produced in the developing apex, a problem which we shall have to take up in a later paper.

DISCUSSION

The most important finding of the present study is the fact that the vascular anatomy of the post-seedling stage is not fundamentally different from the anatomy of the mature vegetative axis. Leaf traces give off numerous bridges ("the anastomosing bridge system") which turn into vertical bundles at the periphery of the central cylinder. The structure of the post-seedling stage is quite confusing at first and it is very doubtful if conventional anatomical methods could have demonstrated it correctly. Only innumerable projections with the data analyzer during which a great number of bundles were followed in both directions finally led to an understanding of the anatomical principles.

The anatomy of the seedling axis of *Rhapis* may shed light on a botanical misconception to which we have drawn attention. Elsewhere (Tomlinson & Zimmermann, 1966a) we have shown that modern ideas about the distribution of vascular bundles in palm stems are erroneous. Diagrams by early investigators implied either a blind ending of vascular bundles at the periphery of the central cylinder when traced downwards, or possibly basal fusion between peripheral bundles. These early workers made it clear that they were undecided on this point. Later writers, often without first-hand familiarity with palm stems, produced diagrams which have become "standard" in modern textbooks in which peripheral fusion of bundles is regarded as a normal feature. But we have shown for *Rhapis* in the first paper of this series, and have much unpublished information about many larger palms, that in the adult aerial axis the continuing vertical bundle is derived from the leaf trace at its point of departure into the leaf. Splitting of vertical bundles in an upward direction (or their fusion if traced downwards) is not a normal property of the adult palm stem although it may occur as a rare abnormality in the center of the rhizome axis.

We have now shown that the inverted cone of the juvenile axis may contain splitting vertical bundles in the periphery of the central cylinder.

This may possibly be a rational explanation for previous botanical misconception of the vascular anatomy of the palm stem. Early workers who studied the juvenile axes might have seen these rare cases in the seedling without appreciating that this is not a property of the adult axis. Among these early workers Falkenberg (1876) and Nägeli (1858) both seem to have studied young plants of *Chamaedorea*. We have reason to believe that Nägeli in particular, who described downward fusion, may have influenced subsequent writers who constructed increasingly hypothetical diagrams of palm stems (Tomlinson & Zimmermann, 1966a).

SUMMARY

In the post-seedling establishment of the adult axis of *Rhapis excelsa* the obconical development at the basal internodes may result in multiplication (in a structural sense) of eight vascular bundles at the cotyledonary node to 400 vascular bundles 10.5 mm. higher. The leaf trace system corresponds closely to that of the aërial stem. Leaf traces give off numerous bridges (the "anastomosing bridge system") which are often quite long, branch, and join neighboring vertical bundles. Branches of the anastomosing system that reach the periphery of the central cylinder become vertical bundles. Since the number of vertical bundles thus produced by each leaf trace is greater than one, the number of vascular bundles in the stem increases. At higher levels the complicated anastomosing system is more and more reduced and the structure approaches that of the mature axis.

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